COWBIRD PARASITISM OF DICKCISSELS IN DIFFERENT HABITATS AND AT DIFFERENT NEST DENSITIES

John L. Zimmerman

When bison (*Bison bison*) grazed the plains, the Brown-headed Cowbird (*Molothrus ater*) lived in commensal association with it (Hamilton and Orians 1965); the lack of territoriality, promiscuous mating system (Elliott 1980), and nest parasitism characteristic of the cowbird are possible adaptations to the nomadic patterns of these large herbivores (Hill 1976). *B. bison* are no longer free-roaming on the prairie and cowbirds have expanded their range with the replacement of the eastern deciduous forest by agronomic communities (Friedmann 1929). They have exploited new hosts (Mayfield 1965) and developed more sedentary behavior patterns (Laskey 1950; Darley 1978, 1982), perhaps in response to the greater availability of host species in the east (Dufty 1982).

In the plains, however, the cowbird has retained its less site-specific behavior and still shows a preference for the "prairie shrub succession" (Lowther and Johnston 1977), those seral communities that would develop in the wake of severe use by large herds of grazers. The Dickcissel (*Spiza americana*) is also adapted to these successional communities (Zimmerman 1971) and to prairie in which herbivore grazing increases forb diversity (Herbel and Anderson 1959), even though suitable nest-sites are fewer (Zimmerman 1982).

As inhabitants of the same communities for so long, the Dickcissel should have evolved to ameliorate the impact of social parasitism on its productivity (Gochfeld 1979). Although the incidence of parasitism is low in peripheral parts of the Dickcissel's current range (Harmeson 1974, Goertz 1977), in the areas of highest densities, the percent of Dickcissel nests parasitized by the cowbird ranges from 31–33% in oldfield habitats (Overmire 1962, Wiens 1963) to 50–53% (Hergenrader 1962, Hill 1976) and even 95% in grazed prairie (Elliott 1978).

Fretwell (1977) has suggested that the introduction of domestic grain crops into the llanos of northern South America at the expense of small-seeded native plants is responsible for the demonstrated difference in survival between male and female Dickcissels during the non-breeding season. The smaller females have experienced a reduction in food availability with the conversion of natural habitats into croplands and have suffered higher mortality so that fewer females return north in the spring. Given the higher incidence of cowbird parasitism in habitats where Dick-

cissels are less abundant, Fretwell (1977) has hypothesized an inverse relationship between host nest density and the intensity of cowbird parasitism. Assuming cowbird parasitism has a depressing effect on host productivity (although this is not always the case, Smith 1981), he further suggested that the increasing impact of cowbird parasitism with decreasing Dickcissel nest density will be the final factor that drives the Dickcissel to extinction once female densities have been sufficiently reduced by the size-related mortality on the wintering range.

The purposes of this paper are: (1) to determine the severity of the impact of the high frequency of cowbird nest parasitism on Dickcissel productivity, (2) analyze the incidence and intensity of parasitism as a function of habitat and the density of host nests, and (3) to assess the productivity of cowbirds in Dickcissel nests.

METHODS

Nest data were obtained from 1965–1979 in oldfield populations on the Ft. Riley Military Reservation and in grasslands on the Konza Prairie Research Natural Area in Riley and Geary counties, Kansas. The two separate oldfield sites were 25.5 km and 12.0 km from the prairie sites. Indeed, the closer oldfield was in sight from the highest ridges on the prairie.

Except for a few populations where nests were visited every 3 or 4 days, most data were gathered by weekly visits to the nests. Week of initiation was known for many nests, but estimated for the majority. For nestlings expected to fledge between visits, the fate of the nests was determined by the female's behavior. At successful nests the female remained in the immediate area feeding the young and giving aggressive displays to my presence. If a nest was lost since the last visit, the female was always gone. The number of fledglings was the number of nestlings at the last visit. Clutch-size data were based on nests assumed to have complete clutches, while all nests found were used to determine the frequency of parasitism and egg success percentages, even though some of these nests failed before egg-laying had been completed. Nesting success data are also presented as survival rates (Mayfield 1961, 1975) with the 95% confidence limits calculated by Johnson's (1979) method.

For three oldfield populations studied in three different years on two plots of 22.7 ha and 30.4 ha and two prairie populations on plots of 28.8 ha and 12.2 ha, concurrent investigations of territoriality and mating patterns provided an intensity of coverage that makes me confident that most nests were found. For these populations, therefore, it was possible to relate the intensity of cowbird parasitism with the density of available nests as well as determine the production of cowbirds per unit area according to habitat. As observed elsewhere in the Great Plains, cowbird egg-laying decreases markedly in July (Wiens 1963, Newman 1970, Hill 1976, Payne 1976) when Dickcissel densities reach their maximum. To compensate for the assumed physiologically-based decline in cowbird egg deposition before that of the Dickcissel, the density analysis was conducted for all weeks up to the week that the density of cowbird eggs/ha fell below 50% of the previous weeks' average. Since only 1.3% of all cowbird eggs laid in prairie nests and only 2.4% of all those in oldfield nests were deposited after the egg-laying period of the host, the density of available nests was determined on just those nests that were under construction or receiving host eggs, those being incubated or brooded were excluded. Nests under construction were included in density calculations for that week as well as in the proportion of nests parasitized even though they might not have received

TABLE 1
MEAN (±SE) COWBIRD EGGS PER PARASITIZED NEST (N)[a] AND PERCENT NESTS PARASITIZED (N)[b] ACCORDING TO WEEK OF NEST START AND HABITAT

Dates	Oldfield		Prairie	
	Cowbird eggs	% parasitized	Cowbird eggs	% parasitized
18–24 May	7.0 (1)[a]	100 (2)[b]	—	—
25–31 May	1.9 ± 0.26 (17)	90 (21)	3.2 ± 0.95 (4)[a]	100 (4)[b]
1–7 June	2.7 ± 0.31 (25)	83 (36)	3.7 ± 0.56 (11)	100 (12)
8–14 June	2.6 ± 0.27 (31)	71 (54)	3.0 ± 0.63 (8)	89 (9)
15–21 June	2.1 ± 0.24 (31)	57 (58)	3.0 ± 0.36 (24)	93 (29)
22–28 June	2.2 ± 0.28 (25)	65 (48)	3.2 ± 0.41 (16)	91 (22)
29–5 July	2.3 ± 0.26 (36)	72 (54)	2.7 ± 0.35 (16)	79 (24)
6–12 July	2.5 ± 0.26 (21)	60 (35)	2.4 ± 0.37 (10)	83 (12)
13–19 July	1.9 ± 0.31 (10)	27 (44)	2.0 ± 0.55 (5)	67 (9)
20–26 July	2.5 ± 0.64 (4)	21 (19)	2.0 ± 0.0 (2)	0 (3)
27–2 Aug.	—	14 (7)	—	0 (1)
3–9 Aug.	—	0 (6)	—	—
10–16 Aug.	—	0 (1)	—	—

[a] N for cowbird eggs based on nests with complete clutches.
[b] N for percent parasitism based on all nests found.

any cowbird eggs until the following week, since nest-building behavior may be an important location cue for the cowbird (Norman and Robertson 1975).

HABITAT DIFFERENCES

Of 385 Dickcissel nests in oldfields, 60.0% were parasitized, while 84.8% of 235 prairie nests were parasitized. This difference is significant (χ^2 = 7.67, df = 1, $P < 0.05$). On a weekly basis, the percent of nests parasitized dropped off earlier in oldfields, finally falling below 50% the week of 13–19 July. In the prairie, the level of parasitism remained higher longer, but similarly fell below 50% after the middle of July (Table 1).

The mean number of cowbird eggs per parasitized nest was also greater in the prairie (Table 1), with weekly means being significantly larger in the prairie during 25–31 May (t = 2.01, df = 19, $P < 0.05$), 1–7 June (t = 1.69, df = 34, $P < 0.05$), and 22–28 June (t = 2.08, df = 39, $P < 0.05$). This difference was also reflected in the larger proportion of multiple cowbird egg clutches in prairies (Fig. 1). While there was no change in the mean number of cowbird eggs in oldfield nests during the nesting season, the mean number laid in prairie nests did significantly decrease with time (b = −0.194, t = 5.51, df = 7, $P < 0.01$), paralleling the drop in the frequency of parasitism.
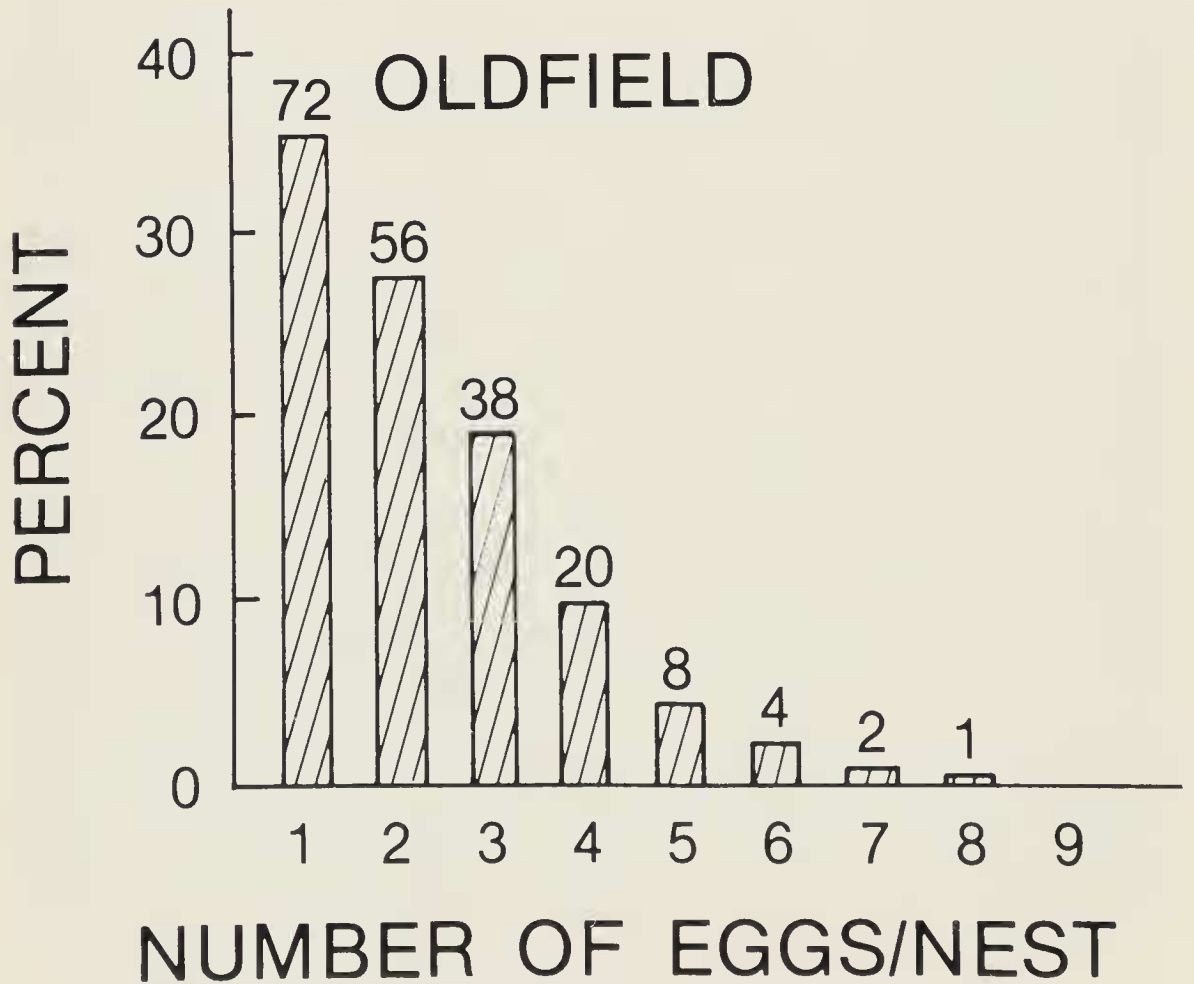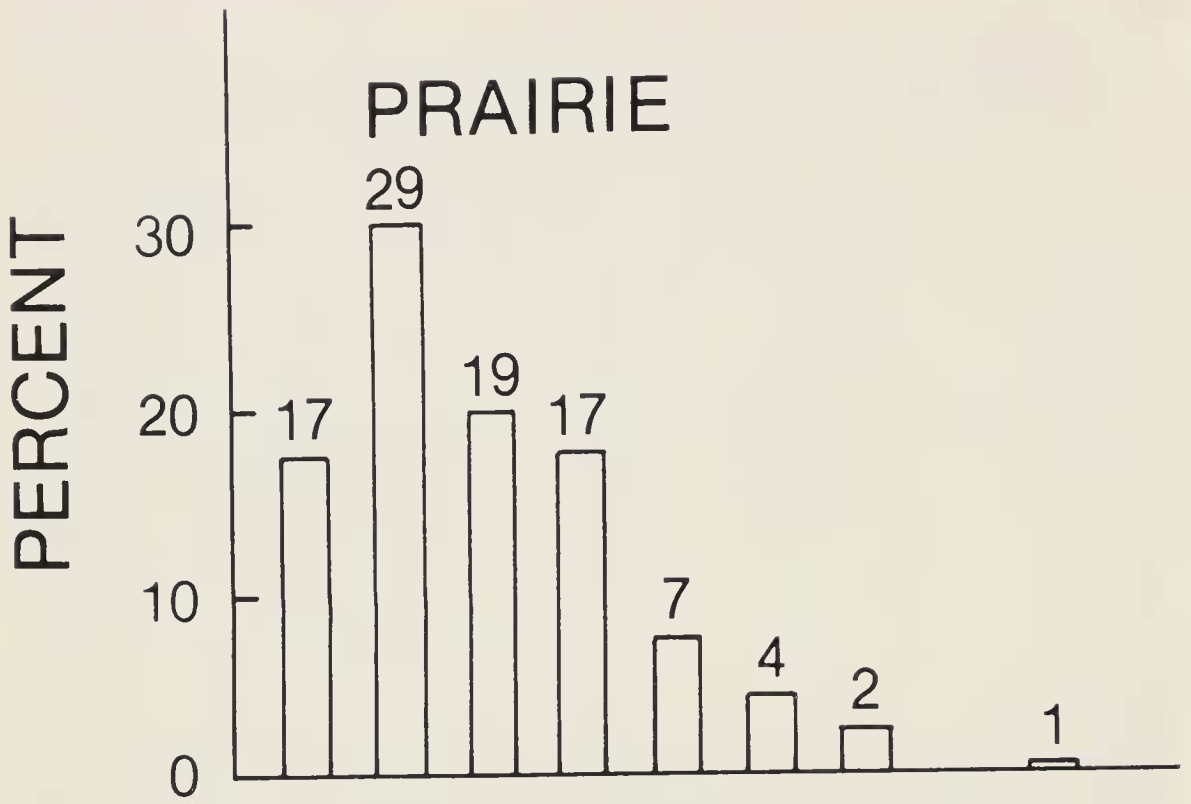
PRAIRIE

PERCENT

30

29

20   19   17

17

10   7

4   2

0   1

OLDFIELD

40

72

PERCENT

30   56

38

20

10   20

8

4   2   1

0

1   2   3   4   5   6   7   8   9

NUMBER OF EGGS/NEST

TABLE 2

MEAN (±SE) INCUBATION TIME[a] OF EGGS VS CLUTCH-SIZE[b]

Eggs in clutch	Mean days of incubation	No. eggs
3	12.3 ± 0.33	3
4	12.0 ± 0.44	22
5	12.0 ± 0.17	15
6	11.5 ± 0.20	34
7	12.4 ± 0.22	10
8	13.2 ± 0.17	6
10	13.7 ± 0.21	6

[a] In days, beginning the day the last egg was laid.
[b] All eggs, including cowbird eggs in parasitized nests.

Since parasitized prairie nests had an increased total clutch-size, incubation times could have been increased due to the inability of the female to maintain an adequately high egg temperature over all the eggs or the need for the female to be off the nest for longer inattentive periods of feeding in response to increased energy demands (Biebach 1981). This would then increase the time the nest would be exposed to predation, decreasing the survival rates of prairie nests. Incubation time (Table 2) was prolonged in larger clutches (Spearman $R = 0.68$, N = 7, $P < 0.06$). But the lengthened incubation period or the increased nest contents had no effect on the daily survival rates of nests since there were no differences according to clutch- and/or brood-size (Table 3).

Some nests were lost by the females' desertion when all host eggs had been removed by cowbirds or when clutch-size became too large, but there was no difference between habitats. Only 8.7% of all prairie nests were abandoned in response to cowbirds (73% of the time this was during the egg-laying period, while the rest were early in incubation). A similar proportion (8.8%) of prairie nests was also abandoned for reasons other than an assumed interference by cowbirds. Among parasitized nests this type of abandonment comprised 6.6% of the total number of nests, while among non-parasitized nests 21.0% were abandoned. In the oldfield, 9.1% of the nests were deserted due to cowbird interference with the majority of these (83%) being abandoned during the egg-laying period. Only 3.6% of the oldfield nests were abandoned for reasons not attributable to cow-

←

FIG. 1. Percent frequency distribution of cowbird eggs per nest in oldfield (cross-hatched) and prairie (open) habitats. Number at top of each bar is the total number of nests with that cowbird clutch in each habitat.

TABLE 3

CLUTCH- AND/OR BROOD-SIZE[a] VS DAILY SURVIVAL RATE ± 95% CONFIDENCE LIMITS
(NO. NESTS)

Clutch- or brood-size	Oldfield	Prairie
1	0.91 ± 0.10 (4)	—
2	0.89 ± 0.07 (10)	—
3	0.91 ± 0.03 (46)	0.97 ± 0.04 (6)
4	0.94 ± 0.01 (110)	0.96 ± 0.03 (22)
5	0.94 ± 0.02 (67)	0.93 ± 0.03 (25)
6	0.96 ± 0.02 (48)	0.94 ± 0.03 (20)
7	0.96 ± 0.02 (17)	0.95 ± 0.03 (18)
8	0.92 ± 0.05 (11)	0.93 ± 0.05 (10)
9–15	0.94 ± 0.03 (17)	0.95 ± 0.04 (12)

[a] Mixed broods of cowbirds and Dickcissels corrected to equal biomass, 1 cowbird young = 1.3 Dickcissel young (Hatch 1975).

birds. Among oldfield parasitized nests, 4.3% were deserted in this way, while 2.6% of non-parasitized nests failed because of abandonment. The proportions of nest desertions as a result of cowbird disturbances in both oldfield and prairie habitats are less than those in "common fosterers" affected by the European Cuckoo (*Cuculus canorus*) (Jourdain 1925:651), as well as lower than observed for the Yellow Warbler (*Dendroica petechia*) (Clark and Robertson 1981) or in the prairie species studied by Elliott (1978). Smith (1981), however, concluded that there was no evidence to attribute nest desertion by Song Sparrows (*Melospiza melodia*) in his population to cowbird activity.
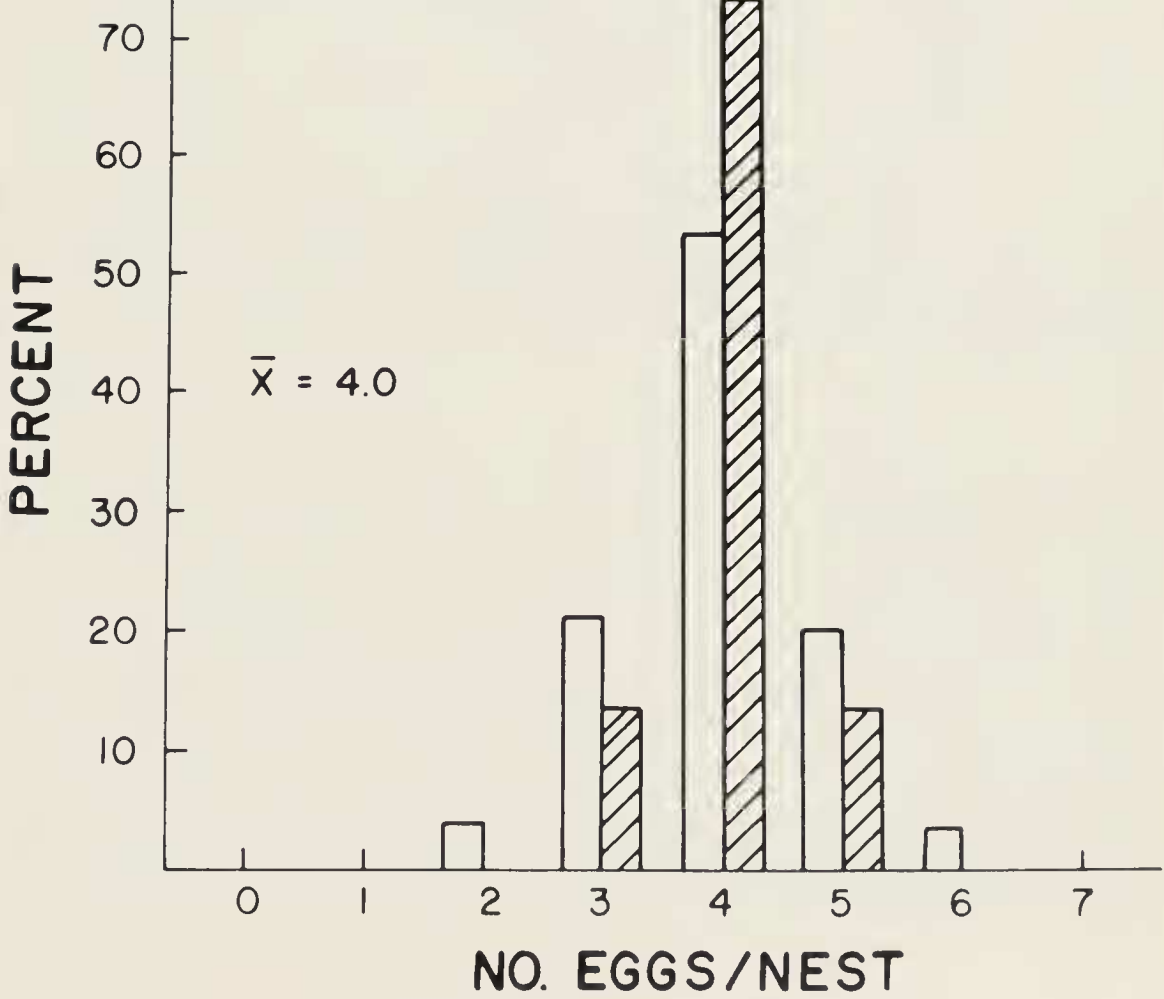
EGG REMOVAL BY COWBIRDS

The frequency distribution of completed clutch-sizes for Dickcissel eggs in both parasitized and non-parasitized nests is illustrated in Fig. 2. The assumption that this difference is due to the removal of eggs by the cowbird from parasitized nests is supported by a single observation of a female cowbird leaving a nest with a Dickcissel egg. There are no significant differences between oldfield and prairie habitats in the mean clutch-sizes of non-parasitized or parasitized nests (Zimmerman 1982); thus, data from both habitats have been combined to estimate the numbers of Dickcissel eggs removed per nest by the cowbird (Fig. 3).

→

FIG. 2.   Percent frequency distribution of Dickcissel eggs per nest in parasitized and non-parasitized nests in oldfield (cross-hatched) and prairie (open) habitats.

PARASITIZED

$\overline{X} = 2.4$

OLDFIELD
PRAIRIE

PERCENT

NON - PARASITIZED

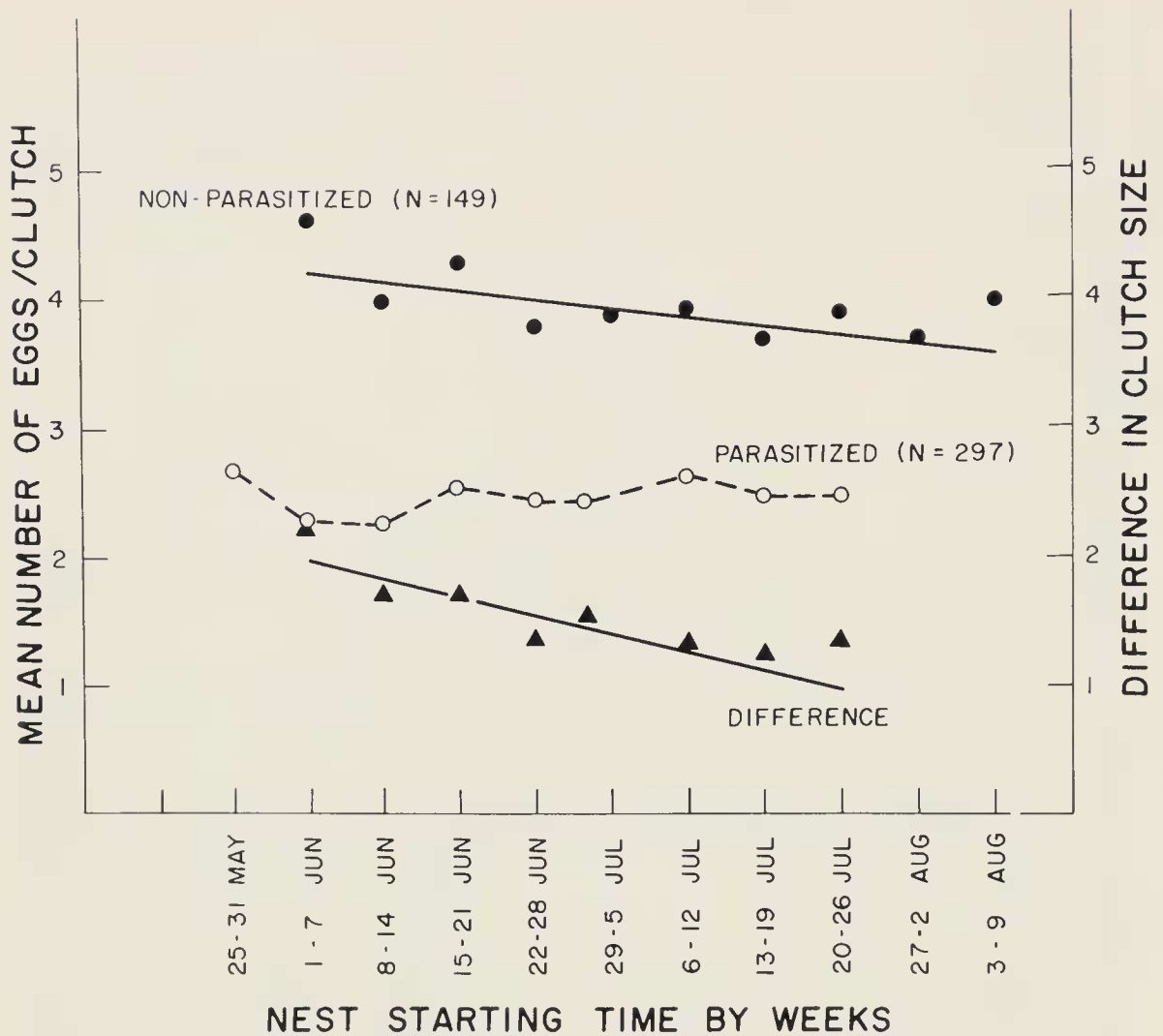$\overline{X} = 4.0$

PERCENT

NO. EGGS/NEST
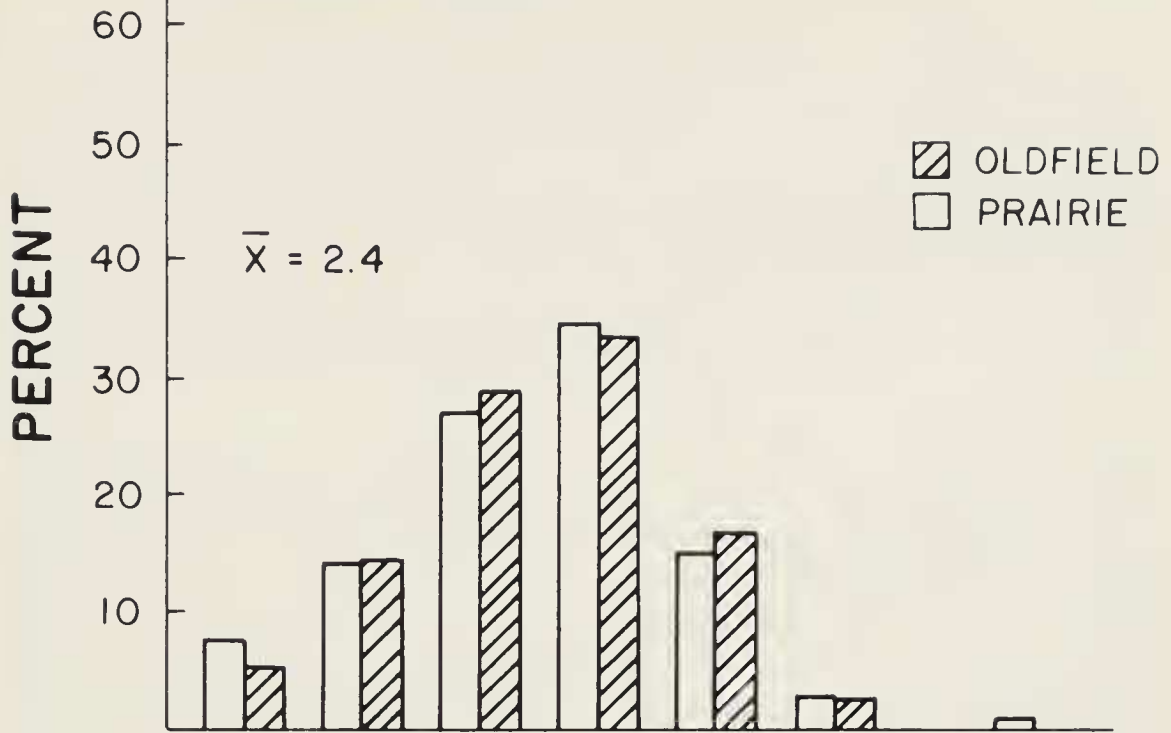
FIG. 3.   Mean number of Dickcissel eggs per nest in non-parasitized (closed circles) and parasitized (open circles) nests combined for both habitats and the difference attributed to egg removal by the cowbird (triangles) according to week of nest starting.

The mean completed clutch-size in non-parasitized nests significantly decreased with nest-starting date ($b = -0.073$, $t = 2.63$, df $= 147$, $P < 0.01$), but there was no temporal change in the numbers of Dickcissel eggs in parasitized nests ($\bar{x} = 2.4$, SE $= \pm 0.06$, N $= 297$). Egg removal was estimated on a weekly basis by subtracting the parasitized clutch-size mean for each week from the corresponding mean for non-parasitized nests. This difference is plotted in Fig. 3, and there is also a significant regression with time of nest start ($b = -0.118$, $t = 4.176$, df $= 7$, $P < 0.01$). Thus, early in the nesting season (late May and June), there were about two Dickcissel eggs removed by cowbirds from each parasitized nest, but this loss decreases to close to one egg per nest by late July. The

median value across all weeks is 1.65 eggs. This is a greater loss than suffered by the American Goldfinch (*Carduelis tristis*) (Middleton 1977), Prairie Warbler (*Dendroica discolor*) (Nolan 1978) or Song Sparrow (Nice 1937), less heavily parasitized hosts inhabiting geographic areas more recently invaded by the cowbird, and closer to Elliott's (1978) estimates based on hatchling counts rather than completed clutches for the Dick-cissel, Grasshopper Sparrow (*Ammodramus savannarum*), and Eastern Meadowlark (*Sturnella magna*) in Kansas grazed prairie.

IMPACT ON PRODUCTIVITY

While the survival rates of Dickcissel nests were not greatly affected by cowbird parasitism, the production of Dickcissels was depressed by the removal of host eggs by the cowbird (Table 4). In oldfields there was a significant difference in the mean number of Dickcissels fledged per suc-cessful non-parasitized nest and the number fledged per successful par-asitized nest ($t = 5.76$, df = 109, $P < 0.01$). Similarly, in prairies the number fledged per successful non-parasitized nest was significantly dif-ferent from the mean number fledged from successful parasitized nests ($t = 4.40$, df = 48, $P < 0.01$). In both habitats there were no significant differences between total young (including cowbirds in parasitized nests) fledged per successful nest when parasitized and non-parasitized were compared. There appears to be a definite (optimum?) number of young (about 3.5) the female can rear (males take no part in parental care, Zim-merman 1966), no matter what the habitat and no matter if some of the young in the brood are cowbirds. Not surprisingly this value is similar to the unparasitized clutch-size of four (Zimmerman 1982).

Table 4 also presents the egg success rates for Dickcissels in oldfield and prairie habitats. The lower fledging success of both Dickcissel and cowbird eggs in oldfields resulted from significantly higher predation rates during incubation compared to the prairie (Zimmerman, unpubl.). The reduction in recruitment calculated according to Payne's (1977) method is 26.9% in oldfields and 29.1% in prairies, values exceeded in Payne's anal-ysis by only the Red-eyed Vireo (*Vireo olivaceous*), a relatively newer host of the eastern deciduous forest. While these two values are not signifi-cantly different, their magnitudes do correspond with the habitat differ-ences in the frequency and intensity of cowbird parasitism.

Using the numbers of eggs remaining in parasitized clutches after the removal of host eggs by the cowbird (246 in prairie nests and 513 in oldfield nests), a comparison with egg success in unparasitized nests might indi-cate detrimental interaction of Dickcissel and cowbird nestlings. For old-fields, 23.0% of the eggs remaining in parasitized nests fledged. If eggs

TABLE 4
Young Fledged per Successful Nest, $\bar{x}$ ± SE (N) and Egg Success

	Prairie	Oldfield
Dickcissels in non-parasitized nests	3.7 ± 0.24 (9)	3.2 ± 0.14 (54)
Dickcissels in parasitized nests	1.8 ± 0.19 (41)	2.0 ± 0.17 (57)
Dickcissels and cowbirds in parasitized nests	3.5 ± 0.20 (41)	3.4 ± 0.17 (57)
Egg success in non-parasitized nests		
Dickcissel laid	63 (18)[a]	550 (151)[a]
Dickcissel fledged	33 (52.4)[b]	170 (30.9)[b]
Egg success in parasitized nests		
Dickcissel laid	419 (105)[a]	891 (229)[a]
Dickcissel fledged	76 (18.1)[b]	118 (13.2)[b]
Cowbird laid[c]	307 (105)[a]	541 (229)[a]
Cowbird fledged	69 (22.5)[b]	84 (15.5)[b]

[a] No. clutches, including incomplete clutches in parenthesis.
[b] Percent of eggs laid that fledged in parenthesis.
[c] No. eggs laid corrected for egg loss by cowbird removal at rate of 1.65 eggs/parasitized nest across all weeks of egg-laying; uncorrected value in prairie = 246, in oldfield = 513.

lost to abandonment in response to cowbird disturbance are accounted for, this value is 24%. Neither of these values is significantly different from the 30.9% egg success rate in unparasitized oldfield nests. In the case of prairie nests, however, only 30.9% of the host eggs remaining fledged and this value is significantly different from the 52.4% egg success in unparasitized prairie nests (χ^2 = 8.83, df = 1, P < 0.01). When eggs lost to cowbird induced abandonment are accounted for, the resulting 32.7% success rate is still significantly different (χ^2 = 6.99, df = 1, P < 0.01).

When the fates of the remaining eggs in prairie nests that did not produce fledglings were compared between parasitized and non-parasitized clutches, predation losses (60 vs 64%), and eggs that did not hatch (17 vs 20%) were similar. Abandonment for unknown reasons and loss of nests from violent weather accounted for 17% of the remaining eggs in unparasitized nests, but only 4% of the eggs in parasitized nests. Unexplained disappearances of eggs and nestlings, on the other hand, were the fate of 12% of the unsuccessful eggs in parasitized nests, while only the cause of 6% of the loss in unparasitized clutches. It does not seem, however, that cowbird parasitism is clearly responsible for the lower success of the eggs remaining after egg removal by cowbirds in parasitized nests. There was

no difference in incubation times between cowbird and Dickcissel eggs that would adversely affect later hatching young. The mean incubation time for 30 cowbird eggs was 12.1 days (SE = ±0.22) and were 12.0 days (SE = ±0.18) for 66 Dickcissel eggs. Hatch (1975) measured growth rates of host young and cowbird young in Dickcissel nests and found no detrimental effect on the growth rate of Dickcissels when compared to their growth rate in unparasitized nests.

COWBIRD PRODUCTIVITY

Scott and Ankney (1980) generalized a fledging success of 15% for cowbird eggs. This is very close to the actual data compiled for oldfield Dickcissel nests in my study (Table 4). The fledging success of cowbird eggs laid in prairie nests was greater and significantly different from the oldfield value (χ^2 = 5.25, df = 1, P < 0.05). This higher probability of a cowbird egg laid in a prairie Dickcissel nest of producing a fledgling, coupled with the greater number of cowbird eggs per prairie nest, resulted in the fledging of 0.65 cowbirds per parasitized nest (SE = ±0.10, N = 106) in the prairie, almost twice as great as the 0.37 cowbirds fledged per parasitized oldfield nest (SE = ±0.05, N = 230). But this higher production of cowbirds per prairie nest is offset by the lower density of host nests. For the prairie populations in which the number of nests found were thought to be quite close to the number actually present, the production of cowbirds was 0.32 fledglings per ha (total area = 41.0 ha). Because of higher nest densities in the oldfield populations, cowbird production was 0.54 fledglings per ha (total area = 75.8 ha). In these oldfields there were only a few Red-winged Blackbirds (*Agelaius phoeniceus*) to serve as alternate hosts in one field and no alternate hosts in the other two fields. In prairies, on the other hand, the availability of alternate hosts is greater (Elliott 1978). But without the nest density values for these alternate hosts it is not possible to compare the suitabilities of the two habitats for the cowbird.

EFFECT OF NEST DENSITY

As was expected, there was a lack of synchrony between the breeding activity of the cowbird and that of the Dickcissel in three oldfield and two prairie populations in which the number of known nests was thought to closely approximate the number actually present (Fig. 4). On the basis of the methods previously described, 26 weekly Dickcissel nest-density values were available from the 43 densities displayed in Fig. 4 and were used to test Fretwell's (1977) hypothesis that the intensity of cowbird parasitism is inversely related to the density of host nests. These weekly nest-
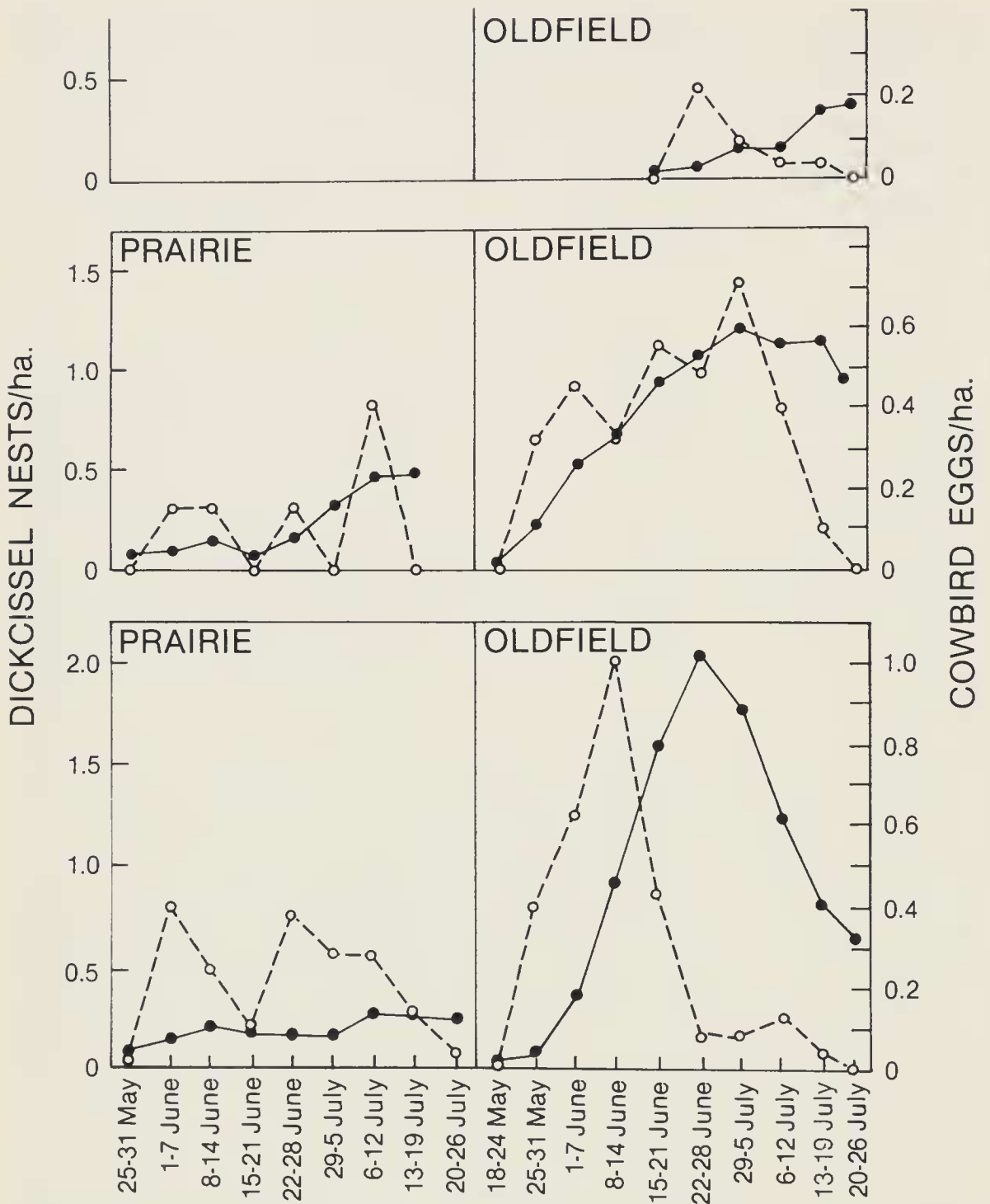
FIG. 4.   Dickcissel nest density (closed circles) and cowbird egg density (open circles) in three oldfield and two prairie populations by week over the period of cowbird parasitism.

density values were analyzed with both the percent of nests newly para-sitized that week and with McGeen's (1972) "cowbird pressure," defined as the product of the percent of parasitism and the frequency of nests with more than one cowbird egg (Table 5).

TABLE 5
Weekly Nest Densities in Oldfields and Prairies, and Cowbird Parasitism

Available nests/ha (N)	% parasitized	% multiple cowbird eggs
0.03 (1)	100	0
0.04 (1)	100	100
0.04 (1)	100	100
0.04 (1)	100	100
0.07 (2)	100	100
0.07 (2)	100	0
0.08 (1)	100	100
0.08 (1)	100	100
0.08 (1)	100	100
0.09 (2)	50	100
0.13 (3)	100	0
0.14 (4)	100	100
0.14 (4)	75	100
0.16 (2)	50	100
0.20 (6)	50	67
0.21 (6)	83	80
0.25 (3)	33	0
0.30 (9)	44	75
0.43 (13)	77	50
0.46 (14)	79	18
0.46 (14)	43	67
0.53 (16)	75	50
0.53 (16)	69	36
0.57 (13)	85	82
0.62 (14)	36	40
0.75 (17)	29	40

Both the frequency of cowbird parasitism and McGeen's (1972) cowbird pressure are significantly and inversely associated with the density of available nests (Spearman $R = -0.774$, N = 26, $P < 0.01$ for frequency; Spearman $R = -0.837$, N = 22, $P < 0.01$ for pressure). These values were calculated from data from both habitats, but evaluation of each habitat separately also demonstrated a significant inverse relationship. Fretwell's (1977) hypothesis that the Dickcissel will suffer heavy cowbird parasitism when nesting densities are reduced is supported by these results. If it is assumed that all other factors affecting Dickcissel recruitment remain at the same level of intensity, then it is perhaps conceivable that extinction of the species might ensue as Fretwell predicts. But predation is still the major cause of nest loss in Dickcissels, and its impact is positively associated with nest density (Fretwell 1977). With lowering nest

densities predation pressure should abate and mitigate the rate of population decline, perhaps permitting regulation at a new, but lower, population level that can be subsequently maintained.

This relationship between nest density and cowbird parasitism also explains the difference in the frequency and intensity of cowbird parasitism between habitats. Nest densities are much lower in prairies than in oldfields due to the greater number of males and the higher incidence of polygyny in oldfield populations (Zimmerman 1971).

SUMMARY

Nest histories from Dickcissel populations in oldfields and prairies of Kansas were analyzed to ascertain the impact of cowbird parasitism on Dickcissel productivity, assess the productivity of Brown-headed Cowbirds in Dickcissel nests, and test Fretwell's (1977) hypothesis that the frequency and intensity of cowbird parasitism were inversely related to host nest density.

Both the frequency and the intensity of cowbird parasitism were significantly greater in prairie populations than in oldfield populations of the Dickcissel. The fledging success of the greater number of cowbird eggs laid per prairie nest was also higher so that almost twice as many cowbirds were fledged from each parasitized prairie nest than were produced from each parasitized oldfield nest.

In both habitats less than 10% of the nests were abandoned in response to cowbird activity. The major effect of parasitism on Dickcissel productivity was the removal of host eggs by the cowbird that resulted in a significant reduction in the numbers of Dickcissels fledged from parasitized nests in both habitats. Early in the nesting season, almost two eggs were removed from each parasitized nest, but this loss decreased to about one egg by mid-July. The reduction in recruitment (Payne 1977) is 26.9% in oldfields and 29.1% in prairies.

Both the frequency of cowbird parasitism and intensity as measured by the "cowbird pressure" (McGeen 1972) were inversely associated with the density of available nests, supporting Fretwell's (1977) hypothesis. This relationship also explains the habitat difference in parasitism since Dickcissel densities were lower in the prairie.

LITERATURE CITED

BIEBACH, H. 1981. Energetic costs of incubation on different clutch sizes in Starlings (*Sturnus vulgaris*). Ardea 69:141–142.

CLARK, K. L. AND R. J. ROBERTSON. 1981. Cowbird parasitism and evolution of antiparasite strategies in the Yellow Warbler. Wilson Bull. 93:249–258.

DARLEY, J. A. 1978. Pairing in captive Brown-headed Cowbirds (*Molothrus ater*). Can. J. Zool. 56:2249–2252.

———. 1982. Territoriality and mating behavior of the male Brown-headed Cowbird. Condor 84:15–21.

DUFTY, A. M. 1982. Movements and activities of radio-tracked Brown-headed Cowbirds. Auk 99:316–327.

ELLIOTT, P. F. 1978. Cowbird parasitism in the Kansas tallgrass prairie. Auk 95:161–167.

———. 1980. Evolution of promiscuity in the Brown-headed Cowbird. Condor 82:138–141.

FRETWELL, S. D. 1977. Is the Dickcissel a threatened species? Am. Birds 31:923–932.

FRIEDMANN, H. 1929. The cowbirds. Thomas, Springfield, Illinois.

GOCHFELD, M. 1979. Brood parasite and host coevolution: interactions between shiny cowbirds and two species of meadowlarks. Am. Nat. 113:855–870.

GOERTZ, J. W. 1977. Additional records of Brown-headed Cowbird nest parasitism in Louisiana. Auk 94:386–389.

HAMILTON, W. J., III AND G. H. ORIANS. 1965. Evolution of brood parasitism in altricial birds. Condor 67:363–382.

HARMESON, J. P. 1974. Breeding ecology of the Dickcissel. Auk 91:348–359.

HATCH, S. 1975. Growth of the Brown-headed Cowbird and hosts at Konza Prairie Research Natural Area in the Kansas Flint Hills. Unpubl. Rept. NSF–URP project.

HERBEL, C. H. AND K. L. ANDERSON. 1959. Response of true prairie vegetation on major Flint Hills range sites to grazing treatment. Ecol. Monogr. 29:171–186.

HERGENRADER, G. L. 1962. The incidence of nest parasitism by the Brown-headed Cowbird (*Molothrus ater*) on roadside nesting birds in Nebraska. Auk 79:85–88.

HILL, R. A. 1976. Host-parasite relationships of the Brown-headed Cowbird in a prairie habitat of west-central Kansas. Wilson Bull. 88:555–565.

JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651–661.

JOURDAIN, F. C. R. 1925. A study of parasitism in the cuckoos. Proc. Zool. Soc. London 1925:639–667.

LASKEY, A. R. 1950. Cowbird behavior. Wilson Bull. 62:157–174.

LOWTHER, P. E. AND R. F. JOHNSTON. 1977. Influences of habitat on cowbird host selection. Bull. Kansas Ornithol. Soc. 28:36–40.

MAYFIELD, H. 1961. Nesting success calculated from exposure. Wilson Bull. 73:255–261.

———. 1965. The Brown-headed Cowbird, with old and new hosts. Living Bird 4:13–28.

———. 1975. Suggestions for calculating nest success. Wilson Bull. 87:456–466.

McGEEN, D. S. 1972. Cowbird host relationships. Auk 89:360–380.

MIDDLETON, A. L. A. 1977. Effect of cowbird parasitism on American Goldfinch nesting. Auk 94:304–307.

NEWMAN, G. A. 1970. Cowbird parasitism and nesting success of Lark Sparrows in southern Oklahoma. Wilson Bull. 82:304–309.

NICE, M. M. 1937. Studies in the life history of the Song Sparrow I. Trans. Linnaean Soc. N.Y. 4.

NOLAN, V., JR. 1978. Ecology and behavior of the Prairie Warbler *Dendroica discolor*. Ornithol. Monogr. 26.

NORMAN, R. F. AND R. J. ROBERTSON. 1975. Nest-searching behavior in the Brown-headed Cowbird. Auk 92:610–611.

OVERMIRE, T. G. 1962. Nesting of the Dickcissel in Oklahoma. Auk 79:115–116.

PAYNE, R. B. 1976. The clutch size and numbers of eggs of Brown-headed Cowbirds: effects of latitude and breeding season. Condor 78:337–342.

———. 1977. The ecology of brood parasitism in birds. Ann. Rev. Syst. Ecol. 8:1–28.

SCOTT, D. M. AND C. D. ANKNEY. 1980. Fecundity of the Brown-headed Cowbird in southern Ontario. Auk 97:677–683.

SMITH, J. N. M. 1981. Cowbird parasitism, host fitness, and age of the host female in an island Song Sparrow population. Condor 83:152–161.

WIENS, J. A. 1963. Aspects of cowbird parasitism in southern Oklahoma. Wilson Bull. 75:130–139.

ZIMMERMAN, J. L. 1966. Polygyny in the Dickcissel. Auk 83:534–546.

———. 1971. The territory and its density dependent effect in *Spiza americana*. Auk 88:591–612.

———. 1982. Nesting success of Dickcissels (*Spiza americana*) in preferred and less preferred habitats. Auk 99:292–298.

DIV. BIOLOGY, KANSAS STATE UNIV., MANHATTAN, KANSAS 66506. AC-CEPTED 5 AUG. 1982.

AARON M. BAGG STUDENT MEMBERSHIP AWARDS

Student Membership Awards in the Wilson Ornithological Society have been made available through funds generously donated in memory of Aaron M. Bagg, a former president of the society. The Student Membership Committee has made the awards for the 1982 applicants and the following students have been given student memberships for 1983 in the Wilson Ornithological Society: Steven R. Beissinger, University of Michigan; Theodore Thomas Buerger, Auburn University; Ann Marie Francis, University of Wisconsin; R. Given Harper, Western Illinois University; Bradley G. Hill, University of Calgary; Lee Richard Jones, Utah State University; Kimberly Dawn Kyker, University of Oklahoma; Brian Alan Maurer, University of Arizona; J. Michael Reed, University of Montana; Dan Alan Roberts, University of North Carolina (Charlotte); Mark Alan Shields, University of North Carolina (Wilmington); Steven Charles Sibley, Mississippi State University; Douglas William White, Rutgers University; Ann M. Wyckoff, University of North Dakota.

Student Membership Committee, Wilson Ornithological Society: Thomas C. Grubb, Charles F. Leck, Roland R. Roth, John L. Zimmerman (chair).